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First finding of an articulated actinopterygian skeleton from the Upper Devonian of Siberia and a reappraisal of the family Moythomasiidae Kazantseva, 1971 (Osteichthyes)

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Abstract. ***Krasnoyarichthys jesseni* gen. et sp. nov. is described from the Upper Devonian (Famennian) of Western Siberia. It is the first finding of a Devonian actinopterygian in Siberia. This new genus is closely related to *Moythomasia*, *Mimia* and *Kentuckia*, but differs from those genera in the relative position of the fins, longer pelvic fin base and other dermal roof bones and scales characters in combination. The family Moythomasiidae with the above-mentioned genera and possibly *Orvikuina* is re-diagnosed and compared.**

Key words: Actinopterygii, Moythomasiidae, systematics, Upper Devonian, Western Siberia.

Introduction

Actinopterygian remains from the Devonian are known usually by isolated scales and disarticulated bones, or by highly incomplete fragments of skeletons; more or less completely articulated specimens are rare. Such remains are known from Western Europe and the Baltic region of Central Europe, Spitzbergen, Afghanistan, North and South America and Australia (Agassiz, 1833–1844; Woodward and White, 1926; Gross, 1942, 1950, 1953; Lehman, 1947; Casier, 1952, 1954; Gardiner, 1963; Berg *et al*, 1964; Jessen, 1968; Schultze, 1968; Gardiner and Bartram, 1977; Pearson and Westoll, 1979; Blieck *et al.*, 1982; Janvier and De Melo, 1987; Long, 1988; Gagnier *et al.*, 1989; Taverne, 1997). Only isolated scales identified as cf. *Moythomasia* sp. were found in Afghanistan (Blieck *et al.*, 1982) and no more or less completely articulated specimens of Devonian actinopterygians were described from Asia. However, a collection of the Paleontological Institute (PIN) in Moscow includes a single nearly complete skeleton from the Upper Devonian deposits of the Krasnoyarski Krai in Western Siberia. This specimen shares many similarities with the genus *Moythomasia* Gross but differs from the latter in several other respects (see below). In the present paper it is described as a new genus and species, *Krasnoyarichthys jesseni*. The family Moythomasiidae Kazantseva, 1971 is reappraised as a consequence of the description of the new taxon.

Notes on geography and stratigraphy

The fossil site is situated 150 km westward from Krasnoyarsk close to Nazarovo City in the southwestern part of the Krasnoyarski Krai (Figure 1). In an abandoned quarry near the Atshinsk-Abakan railroad, brown sandstones are exposed interrupted by calcareous alveolites with rare concretions. These layers belong to the Famennian Stage (Sidorenko, 1964). The specimen was found in a concretion.

Systematic paleontology

Order Cheirolepiformes
(sensu Kazantseva-Selezneva, 1977)
Family Moythomasiidae Kazantseva, 1971

Emended diagnosis. — Relatively small fishes with fusiform body. Frontal bones as long as or 1.7 times longer than parietals. Both intertemporal and supratemporal present [intertemporal is not documented in *Kentuckia*, however, it might be present according to its reconstruction (Rayner, 1951, p. 56)]. Supratemporal not contacting frontal. Antorbital and single supraorbito-infraorbital present. Postorbital portion of maxillary well

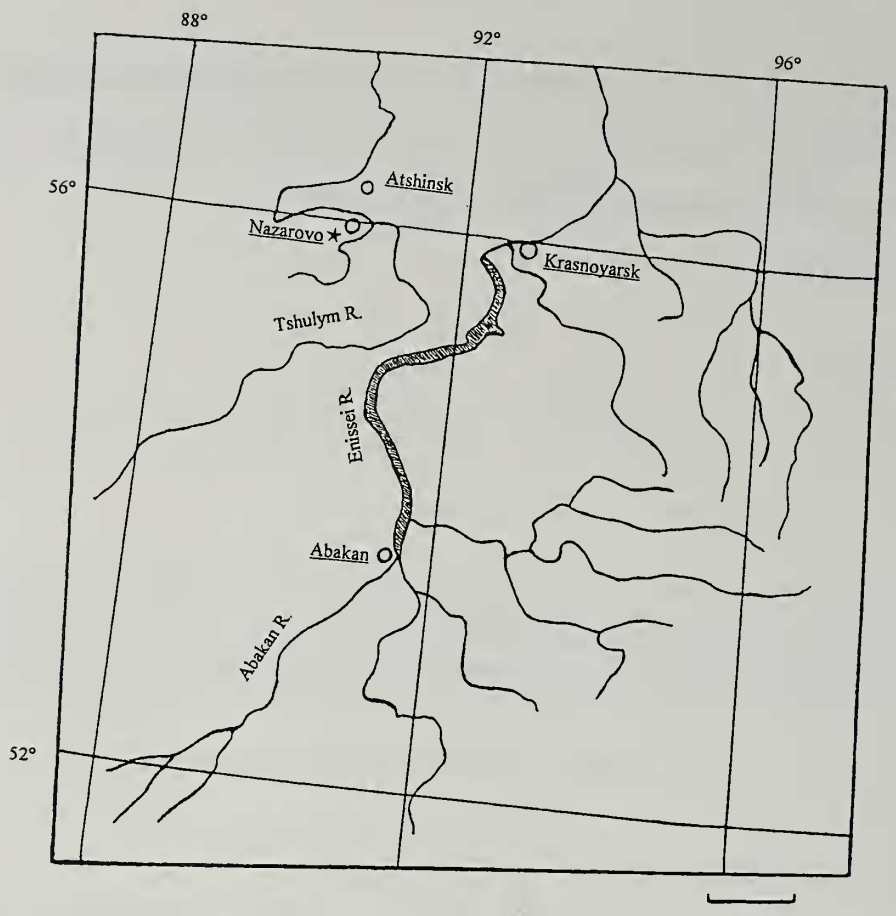

Figure. 1. Map of a section of Western Siberia illustrating the location of the fossil site (★). Scale bar 75 km.

developed. Mandibular suspension oblique. Both dermohyal and epipreopercle present, completely separating opercle and preopercle. Preopercle with two branches. Opercle larger than subopercle. Skull roofing bones ornamented with longitudinal ridges of ganoine. All fins with minute fringing fulcra and with rays articulated and distally bifurcating. Dorsal and anal fins completely or partially opposite to one another; anal fin originating on the same level as the dorsal fin origin or behind it. Pelvic fin base shorter than anal fin base. Caudal fin heterocercal. Dorsal and ventral ridge scutes present. Scales ornamented with diagonal ridges which end on the posterior scale margins as a series of serrations; all body scales with peg-and-socket articulations.

Included genera.—*Moythomasia* Gross, 1950 (Middle-Upper Devonian, Western and Central Europe, ?Afghanistan, Western Australia); *Kentuckia* Rayner 1951 (Lower Carboniferous, USA); *Mimia* Gardiner and Bartram 1977 (Upper Devonian, Western Australia); *Krasnoyarichthys*, gen. nov. (Upper Devonian, Western Siberia); possibly also *Orvikuina* Gross, 1953 (Middle Devonian, Central Europe), which is known only by isolated scales.

Krasnoyarichthys gen. nov.

Type species. — *Krasnoyarichthys jesseni*, sp. nov.; monotypic genus.

Etymology.—From the Krasnoyarsky Krai, and-*ichthys* (Greek), fish; masculine.

Diagnosis.—Same as that of the type species.

Krasnoyarichthys jesseni sp. nov.

Holotype.—PIN, nr. 4890–1, nearly complete skeleton lacking snout, anterior parts of the skull roof and of the cheek, and caudal fin, with poorly preserved cephalic sensory canals and limits of scales on the caudal peduncle; single plate (Figure 2a); Western Siberia, Krasnoyarski Krai, vicinity of Nazarovo City, Preobrazhensky Village, quarry near railroad; Upper Devonian (Famennian). Species is known only by the holotype.

Ethymology.—Species named in honour of Hans Jessen for his great contribution to palaeoichthyology.

Diagnosis. — Relatively small fishes reaching a total length of about 10 cm. Maximum body depth contained

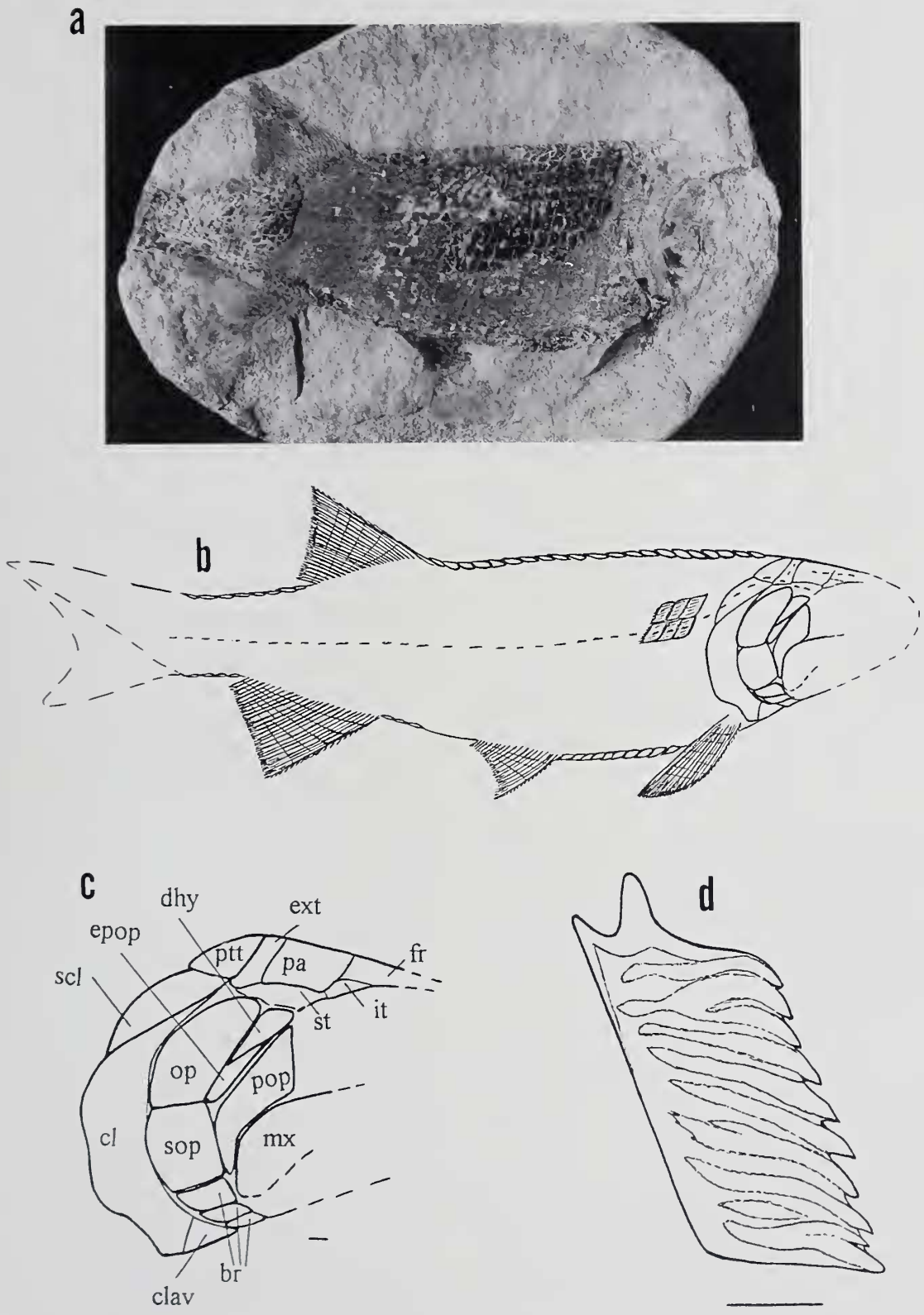

Figure. 2. *Krasnoyarichthys jesseni* gen.' et sp. nov., Upper Devonian (Famennian) of Krasnoyarski Krai (Siberia). **a**. Holotype, PIN, nr. 4890–1 (natural size). **b**. Reconstruction of the lateral view. **c**. Reconstruction of the postorbital part of the skull and of the pectoral girdle (as the cephalic sensory canals are poorly preserved they are omitted in figure). **d**. Isolated scale from left side of body. Scale bars 1 mm. Abbreviations: br, branchiostegal rays; cl, cleithrum; clav, clavicle; dhy, dermohyal; epop, epipreopercle; ext, extrascapular; fr, frontal; it, intertemporal; mx, maxillary; op, opercle; pa, parietal; pop, preopercle; ptt, posttemporal; scl, supracleithrum; sop, subopercle; st, supratemporal.

approximately 3.5 times in the total length. Extrascapular single on each side of skull, two times larger than long. Postorbital portion of maxillary deep. Opercle 1.5 times deeper than long. Subopercle 1.5 times smaller than opercle. Pelvic fin originating equidistantly from the pectoral and anal fin origins; pelvic base only 1.5 times shorter than anal fin base. Dorsal fin origin in front of that of anal fin; posterior edge of anal fin noticeably behind that of dorsal fin. Approximate numbers of fin-rays: dorsal 40, anal 40, pelvic 30, pectoral 30. Roofing bone ornament consisting of coarse longitudinal and diagonal ridges of ganoine. Scales rhomboidal, ornamented by up to 10 diagonal ridges which end on posterior scale margins as series of serrations. Middle trunk scales approximately twice, or less, deeper than long. Dorsal and ventral ridge scutes weakly developed.

Description (Figure 2).—Besides the characters given in the diagnosis there are several additional features. The estimated standard length of the holotype is approximately 100 mm. Measurements in mm: length from the posterior border of the cleithrum to the caudal base 76, length from the posterior border of the cleithrum to the dorsal fin origin 41, the same length to the anal fin origin 46, the same length to the pelvic fin origin 24, distance between the pectoral and pelvic fin origins 26, distance between the pelvic and anal fin origins 26, maximum body depth 32, caudal peduncle depth 8, dorsal fin base length 16, anal fin base length 16, pelvic base length 11, dorsal fin height 20, anal fin height 18, pelvic fin height 9, pectoral fin height 11. The transverse rows of scales on the body are approximately 50 in number. There are 16 longitudinal rows of scales on the body. The dorsal ridge scutes are continuous from the occiput to the dorsal fin origin, and between the dorsal and caudal fins. The ventral ridge scutes are between pectoral and pelvic fins, and between anal and caudal fins; at least three slightly enlarged ventral scales are present before anal fin origin.

Discussion

Based on its similar body form, position of the fins, cranial roofing bones and structure of the scales *Krasnoyarichthys* undoubtedly belongs to the family Moythomasiidae. However, the new genus differs from both *Moythomasia* and *Mimia* in the relative position of the dorsal and anal fins (dorsal fin origin and ending in front of those of anal fin vs. dorsal and anal fins opposite one another in the compared genera) and in the slightly longer pelvic fins (1.5 times in the length of the anal fin base vs. twice in the compared genera). It further differs from *Moythomasia* in the presence of a single extrascapular on each side of the skull (vs. two in *Moythomasia*), which is noticeably larger than long (the extrascapulars are approximately as large as long in *Moythomasia*). *Krasnoyarichthys* is distinguished from *Mimia* in the middle trunk scales being no more than twice times deeper than long (vs. 3–4 times deeper than long in *Mimia*) and in the much less prominent ridge scutes. The new genus differs from *Kentuckia*, which is known only by the skull, in the opercle 1.5 times (vs. 2.5 times) deeper than long and 1.5 times (vs. twice) larger than the subopercle, and in the deep postorbital portion of the maxillary. The new genus is distinct from *Orvikuina*, which is known only by isolated scales, in having scales deeper than long (vs. much longer than deep), bearing up to 10 serrations (vs. 2–3 in *Orvikuina*).

The family Moythomasiidae is neglected in the literature. The genus *Moythomasia* together with *Kentuckia* Rayner and *Stegotrachelus* Woodward and White were placed by Gardiner (1963) in the family Stegotrachelidae. Later, Gardiner and Bartram (1977) added the genus *Mimia* to this family. However, the subsequent reconstruction of *Moythomasia* published by Jessen (1968) shows numerous distinctions between the latter and *Stegotrachelus*. Kazantseva (1971) indicated the principal differences between *Stegotrachelus* and *Moythomasia* were in the structure of the bones of the cheek region (both dermohyal and epipreopercle are absent in *Stegotrachelus*) and transferred *Moythomasia* and *Kentuckia* to another family, the Moythomasiidae. Unfortunately, this decision was never discussed by other authors (Gardiner, 1984; Gardiner and Schaeffer, 1989; Taverne, 1997).

In their phylogenetic analysis of the basal actinopterygians, Gardiner and Schaeffer (1989) placed *Mimia* and *Tegeolepis* into a «*Mimia* group», and *Moythomasia*, *Howqualepis* and *Stegotrachelus* into a «*Moythomasia* group»; the «*Mimia* group» was considered as a sister taxon for the «*Moythomasia* group» plus other actinopterygians excluding *Cheirolepis* and the polypterids. Unfortunately, this analysis is based on many characters not preserved in numerous paleoniscoid groups known to date (i.e. characters of the neurocranium, pectoral and pelvic girdles, axial skeleton, etc.), and their phylogenetic significance therefore needs further elucidation. In our opinion, the structure of the dermal skull bones provides the most important data for elucidation of paleoniscoid relationships, because they are always preserved in fossils and indicate the different evolutionary trends (Kazantseva-Selezneva, 1981). The only dermal bone character mentioned by Gardiner and Schaeffer (1989) as common to *Stegotrachelus* and *Moythomasia* is the absence of a true dermopterotic. The *Cheirolepis*, *Mimia* and *Moythomasia* groups of Gardiner and Schaeffer (1989) have no dermopterotic but two bones (intertemporal and supratemporal) in this region of the skull. However, in Gardiner's (1963: 296, fig. 12) reconstruction of the

Stegotrachelus skull the intertemporal is not figured. The other dermal skull characters of *Stegotrachelus* [absence of accessory opercular bones, long supratemporal (or dermopterotic) contacting frontal, small parietals, very narrow extrascapulars, numerous suborbitals] clearly distinguish the latter from the other members of the above-mentioned groups. According to Kazantseva-Selezneva (1981), the family Moythomasiidae seems to be closely related to the Cheirolepididae and Cosmoptychiidae rather than to the Stegotrachelidae. On the other hand, Taverne (1997) considered all the Devonian genera, *Cheirolepis* and *Dialipina* excluded, as the sister group of «polypteriforms». This opinion is doubtful judging from the close relationships between the Polypteridae and the peculiar Triassic Scanilepiformes (Sytchevskaya, 1999), and Lund's (2000) cladistic analysis of the polypteriforms which has specified sister relationships between the polypterids plus guildayichthyiforms and the platysomiforms.

According to Kazantseva (1971, 1974a, 1974b, 1977, 1981), the presence or absence of the dermohyal and epipreopercle is highly significant for the higher classification of the paleoniscoid fishes and indicates different types of breathing. Kazantseva-Selezneva (1977, 1981) divided the order Palaeonisciformes into three separate orders (Cheirolepiformes, Elonichthyiformes and Palaeonisciformes s. str.), of which both the dermohyal and epipreopercle are present only in the Cheirolepiformes. Among the Cheirolepiformes, the structure of the cranial roofing bones of the Moythomasiidae is similar to that in the Cheirolepididae. Both families have a single supraorbito-infraorbital, large parietals, the supratemporal lacking contact with the frontal bone, and the preopercle and opercle completely separated by the dermohyal and epipreopercle. However, the Cheirolepididae sharply differ from the Moythomasiidae in the structure of their scales, which are minute, square, not overlapping, with an internal boss, and quite similar to those of the acanthodians in the Cheirolepididae (contrary to the typical palaeoniscoid scales of the Moythomasiidae). The other distinctions include the presence of a separate antorbital in the Moythomasiidae [vs. completely fused with the premaxillary into the rostro-premaxillo-antorbital bone (Gardiner, 1963; Pearson and Westoll, 1979)], the anal fin origin opposite the dorsal fin origin or just behind it in the Moythomasiidae (vs. in advance of the dorsal fin origin in the Cheirolepididae), the pelvic base shorter than the anal base, and the ridge scutes present in the Moythomasiidae (in contrast to the reverse conditions in the Cheirolepididae) and the body form less elongate in the Moythomasiidae.

In our opinion, the family Moythomasiidae is valid and closely related to the Cheirolepididae. Such cranial characters as long parietals, presence of intertemporals, supratemporals lacking contact with frontal bones, single infraorbito-suborbital, and dermohyal and epipreopercle completely separating the preopercle from the opercle characterising both these families seem to be primitive, according to the undoubted position of *Cheirolepis* as the most primitive actinopterygian (Berg *et al.*, 1964; Pearson and Westoll, 1979; Patterson, 1982; Lauder and Liem, 1983; Gardiner and Schaeffer, 1989; etc.). The orbit relatively larger with regard to the overall body size, the shorter body, the short-based pelvic fins, the presence of peg-and-socket scale articulations on the body scales and ridge scutes on the body contours indicate the advanced status of the Moythomasiidae. The peculiar Australian genus *Howqualepis* has small orbits, a long body, and long-based pelvic fins, and it lacks dorsal and ventral ridge scutes, which establishes its similarity to *Cheirolepis*; however, the supratemporal has contact with the frontal and the parietals are two times shorter than the frontals in *Howqualepis* (Long, 1988). All these characters undoubtedly exclude *Howqualepis* from the Moythomasiidae. The other Devonian genera (*Dialipina* and *Ligulalepis*, which are known only by isolated scales; *Osorioichthys* and *Tegeolepis*) sharply differ from the Moythomasiidae in the cranial and scale characters and the two latter belong to other families (Osorioichthyidae and Tegeolepididae, respectively) (Schultze, 1968; Gardiner, 1963, 1967; Kazantseva-Selezneva, 1977, 1981).

Conclusion

Krasnoyarichthys jesseni gen. et sp. nov. from the Upper Devonian (Famennian) of Western Siberia belongs to the family Moythomasiidae, and differs from the other members of this family in the following combination of characters: single extrascapular on each side of the skull, which is noticeably larger than long; deep postorbital portion of maxillary; opercle 1.5 times deeper than long and 1.5 times larger than the subopercle; dorsal fin origin in front of that of anal fin; posterior edge of anal fin noticeably behind that of the dorsal fin; pelvic fin base 1.5 times in the anal fin base length, and middle trunk scales no more than twice deeper than long. The family Moythomasiidae presently is recognized as distinct and closely related to the Cheirolepididae, on the basis of their similar cranial roofing bone characters. However, the moythomasiids seem to be more advanced than the cheirolepidids judging from their relatively larger orbit with regard to the overall body size, shorter body, short-based pelvic fins, the presence of peg-and-socket scale articulations on the body scales and ridge scutes on the body contours.

The moythomasiids and other Devonian actinopterygians are recorded in marine sediments only (Jessen, 1968; Schultze, 1968; Gardiner, 1984; Janvier and De Melo,

1987; etc.), and Sidorenko (1964) noted a marine origin for the deposits, in which the holotype of *Krasnoyarichthys* subsequently was found. This taxon is the first finding of the Moythomasiidae in Siberia. Further investigations of the Preobrazhensky fossil site are needed since they have special interest for the morphology, taxonomy and paleobiogeography of Devonian actinopterygians.

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Errata

In the article by Takashi Matsubara (*Paleontological Research*, Vol. 6, No. 2, pp. 127–145), the following corrections should be made:

page	table/column	line	read	for
130	Table 1	9	*Acila* (*Truncacila*) cf. *nagaoi*	*Acila* (*Truncacila*) cf. nagaoi
130	Table 1	11	*Glycymeris* (*Glycymeris*) sp.	*Glycymeris* (*glycymeris*) sp.
130	Table 1	15	*Clılamys* (*Leoclılamys*) *namigataensis*	*Chlamys* (*leoclılamys*) *namigataensis*
130	Table 1	16	*Crassostrea* sp.	*Crassastrea* sp.
130	Table 1	17	Lucinidae gen. et sp. indet.	Luchinidae gen. et sp. indet.
130	Table 1	18	*Cyclocardia* sp.	*Cyclocardin* sp.
130	Table 1	20	*Megangulus maximus* (Nagao)	*Megangulus maximus* (Nagano)
141	Left	44	[delete]	Fo
141	Left	45	Formation	rmation
142	Left	4	Activities, Hyogo/Himeji Institute	Activities, Hyogo Himeji Institute
143	Right	7	*Editio duodecima*	*Editio decima*
144	Right	21	*siciliale*	*Siciliale*
144	Right	23	*Tome 2*	Tom 2
144	Right	30	*Pars secunda*, viii+199 p.	*Pars Secunda*, viii-199p.

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